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Published in:
Condor

DOI:
[10.2307/1368193](https://doi.org/10.2307/1368193)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
1991

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Klaassen, M., & Drent, R. (1991). An analysis of hatchling resting metabolism: In search of ecological correlates that explain deviations from allometric relations . *Condor*, 93(3), 612-629.
<https://doi.org/10.2307/1368193>

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Source: *The Condor*, Vol. 93, No. 3 (Aug., 1991), pp. 612-629

Published by: American Ornithological Society

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AN ANALYSIS OF HATCHLING RESTING METABOLISM: IN SEARCH OF ECOLOGICAL CORRELATES THAT EXPLAIN DEVIATIONS FROM ALLOMETRIC RELATIONS¹

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Abstract. From data in the literature, an allometric equation is compiled for hatchling resting metabolic rate and an attempt is made to explain residual variation in terms of hatchling type, yolk and water content, embryonic and postnatal growth rate, and environmental circumstances (latitudinal distribution). The body mass exponent for resting metabolism in hatchlings was 0.86 and, thus, substantially different from the values compiled for adult birds (0.67–0.75). Relatively high hatchling metabolic rates were found for birds exhibiting high embryonic and postnatal growth rates, as well as for those species that hatched at high latitudes. A functional explanation is postulated for the correlations between hatchling metabolism and these three variables.

Key words: *Hatchling; resting metabolic rate; allometric relation; hatchling type; growth rate; latitude; chick energetics.*

INTRODUCTION

Birds enter their world under varying circumstances: close to the poles the tiny neonates have to cope with extreme cold, whereas in the tropics they must deal with high temperatures and possible overheating. Superimposed on these thermal challenges of the environment is the unpredictability of the food supply. Neonates differ in many respects, categorized in the familiar dichotomy of altricial/precocial or the more refined gradient proposed by Nice (1962). Attempts to unravel adaptive responses governing avian ontogeny have suffered from the lack of a frame of reference. It is our conviction that resting metabolic rate can, in fact, provide a standard of comparison, and we will seek to show that adaptive responses in the level of metabolism do exist and transcend the ontogenetic classification.

Historically, the search for an allometric relationship of resting metabolic rate with body mass valid for all birds was the goal. Starting with Brody and Proctor (1932), resting metabolic rate has been measured extensively in adults and many analyses have defined the relationship between this measure of metabolism and body mass. However, it was not until recently that deviation from allometric equations of resting metabolism

for specific groups of birds, species, or even individuals claimed attention. Often these metabolic deviations are related to phylogeny in addition to the specific physiology, morphology, behavior and ecology of the adult birds (e.g., Ellis 1984; Kersten and Piersma 1987; Bennett and Harvey 1987; McNab 1988; Daan et al. 1989, 1990).

During growth, an individual animal changes drastically in an array of ways. To ease interpretation of the variation in resting metabolism between species, one prerequisite is that the animals in the analysis should be in a comparable developmental state. Hatching is a well-defined time point during growth from zygote to adult and is a logical choice. So far, analyses of hatchling resting metabolism have been restricted to relatively few bird species and have dealt with only a few possible correlates (e.g., Ackerman et al. 1980; Dawson and Bennett 1980; Bryant and Hails 1983; Bucher 1983, 1986, 1987; Brown and Adams 1988; Drent and Klaassen 1989; Klaassen et al. 1989a, 1989c). In this review, we determine an allometric equation from the data now available on hatchling resting metabolism. In addition, we provide an interpretation of deviation in metabolic rate from predicted values in the light of some specific physiological, morphological, behavioral and ecological characteristics of the hatchlings (namely: ontogenetic type, water and yolk content, embryonic and postnatal growth rate) and environmental circumstances

¹ Received 17 December 1990. Final acceptance 8 May 1991.

(latitude) which may determine their specific level of metabolism.

METHODS

A difficulty in defining resting metabolic rate in an actively growing hatchling is that it may rarely, if at all, be in a truly post-absorptive state due to use of yolk reserves (Klaassen et al. 1987). We use for hatchling resting metabolism (RMR_h , ml O_2 day⁻¹) the mean minimal values of oxygen consumption obtained when unfed hatchlings are at rest under presumed thermoneutral conditions. Table 1 summarizes published data on hatchling resting metabolism and various variables to which the level of hatchling metabolism might be related: fresh body mass (M , g), yolk-free dry body mass (M_{yfd} , g), embryonic growth rate (K_e , g day⁻¹), postnatal growth rate (Gompertz K , K_G , day⁻¹, Ricklefs 1967a), asymptotic body mass (A , g), latitude (L , °N or °S) and hatchling type (HT, according to Nice, 1962). Values were used only when both hatchling resting metabolism and fresh body mass were available. Embryonic growth rate is here defined as hatchling fresh body mass divided by incubation length. Nice (1962) describes eight categories of maturity based upon morphological and behavioral criteria, and we numbered all these classes denoting the most precocial with 1 and altricial with 8 (recording of Nice's classification: 1 = P1, 2 = P2, 3 = P3, 4 = P4, 5 = SP, 6 = SA1, 7 = SA2, 8 = A). Nice (1962) labelled the Procellariiformes semialtricial but we departed from this classification by considering them semiprecocial as has become common practice in recent literature (e.g., Ricklefs et al. 1980; Bucher 1986, 1987; Vleck and Vleck 1987). Precocial hatchlings typically contain more yolk and less water than altricial hatchlings (Romanoff 1944; Nice 1962; Ricklefs 1974, 1977; Blem 1976; Ar and Yom-Tov 1978; Ricklefs et al. 1978; Ar and Rahn 1980; Carey et al. 1980; Carey 1983; Pettit et al. 1984b; Rahn et al. 1984; Sotherland and Rahn 1987). As both yolk and water are metabolically inactive, and correction for these components could make hatchlings of different developmental types metabolically more comparable on a mass-specific basis (as proposed by Vleck and Vleck 1987), the yolk-free-dry body mass was also used in calculations. For the cases in which references had to be combined in order to obtain a complete data set for a given species, only the latitude at which hatchling resting metabolism

was measured was used. For Arctic Tern (*Sterna paradisaea*) and Common Eider (*Somateria mollissima*), hatchling resting metabolism measurements at two localities at widely separated latitudes were available. For domestic animals and hatchlings for which the embryonic development had taken place mainly in an incubator and possible latitude-related temperature effects (see discussion) might have been masked, latitude was not entered. The data set is subdivided into 14 phylogenetic groups (12 orders of which the Charadriiformes are divided into 3 family groups).

It is well established that metabolic rate increases exponentially with body mass (Peters 1983). Therefore, allometric equations were obtained from least-square linear regression of log-transformed data. Since embryonic and postnatal growth rates show a pattern when considered in relation to body mass, many attempts have been made to investigate this interrelation in search of predictive generalities (Ricklefs 1968, 1973, 1979, 1987). Therefore, embryonic growth rate was regressed on hatchling fresh body mass and postnatal growth rate was regressed on asymptotic body mass (after logarithmic transformation).

To obtain mass-independent estimates of hatchling resting metabolism, embryonic growth rate and postnatal growth rate, the measurements were divided by the values predicted with the allometric equations. With this set of standardized values, variation in hatchling metabolism, independent of body mass, could be related to: latitude, hatchling type, and mass-independent estimates of embryonic and postnatal growth rates.

RESULTS

The relation of hatchling resting metabolism (ml O_2 day⁻¹) on fresh body mass (g) is:

$$\log(RMR_h) = 1.697 + 0.855 \log(M) \quad (1)$$

($r = 0.959$, $P < 0.001$, $n = 84$; Fig. 1). Analysis of covariance reveals a significant effect of phylogeny on the relation between hatchling resting metabolism and fresh body mass ($F = 4.219$, $P < 0.001$). Therefore, allometric relations between hatchling resting metabolism and hatchling fresh body mass are also compiled for the phylogenetic groups containing at least 6 data points (Table 2).

TABLE 1. Hatchling type (HT), latitude (L, °N or °S), embryonic growth rate (K_e , g day⁻¹), postnatal growth rate (K_G , day⁻¹), asymptotic body mass (A, g), hatchling yolk-free dry body mass (M_{yfd} , g), hatchling fresh body mass (M, g) and hatchling resting metabolism (RMR_h , ml O₂ day⁻¹) for 82 (sub-) species of birds divided over 14 phylogenetic groups.

Species	HT	L	K_e	K_G	A	M_{yfd}	M	RMR_h	Authors
Order Sphenisciformes									
<i>Pygoscelis adeliae</i>	7	65	2.31	0.093	3,595	11.6	80.7	2,189	1, 2
<i>Pygoscelis antarctica</i>	7	62		0.072	4,691		78	2,415	3
<i>Pygoscelis papua</i>	7	62		0.055	5,976		88.5	2,301	3
Order Struthioniformes									
<i>Struthio camelus</i>	3		19.2				885	8,448	4
Order Rheiformes									
<i>Rhea americana</i>	3		10.3				400	4,013	4
Order Casuariiformes									
<i>Dromaius novaehollandiae</i>	3		8.50				425	4,265	4
Order Procellariiformes									
<i>Diomedea exulans</i>	5	45	4.14	0.018	12,000		331	8,058	5, 6
<i>Diomedea immutabilis</i>	5	28	3.25	0.016	3,200	39.93	208	3,820	6, 7, 8
<i>Diomedea nigripes</i>	5	28	3.31	0.022	3,200	40.66	215	3,680	6, 7, 8
<i>Macronectus giganteus</i>	5	45	3.63				214	5,048	5
<i>Oceanodroma furcata</i>	5	59	0.22				8.2	250	9
<i>Oceanodroma leucorhoa</i>	5	47	0.17	0.074	75		7.3	420	6, 10, 11
<i>Pachyptila desolata</i>	5	54	0.60				27	1,290	12, 13
<i>Pachyptila vittata salvini</i>	5	45	0.88				28	941	5
<i>Pelecanoides georgicus</i>	5	54	0.36				16.7	601	12, 13
<i>Pelecanoides urinatrix</i>	5	54	0.29				15.5	673	12, 13
<i>Procellaria aequinoctialis</i>	5	45	1.56				91	3,079	5
<i>Pterodroma hypoleuca</i>	5	28	0.66	0.054	250	6.16	31.8	757	7, 14, 15
<i>Pterodroma macroptera</i>	5	45	1.57				83	1,733	5
<i>Puffinus pacificus</i>	5	21	0.75	0.043	390	7.13	39.1	840	6, 7, 16
<i>Puffinus puffinus</i>	5	62	0.61	0.069	650		31	1,280	6, 17
<i>Thalassoica antarctica</i>	5	72		0.071	735		63.2	2,343	18, 19
Order Pelecaniformes									
<i>Pelecanus occidentalis</i>	8	8	2.36	0.071	4,000	9.08	72	1,060	6, 20, 21
Order Anseriformes									
<i>Anas crecca</i>	2	61	0.76				16.8	279	19, 22
<i>Anas penelope</i>	2	61	1.06				26.4	1,007	19, 22
<i>Anas platyrhynchos</i>	2	61	1.07	0.057	950	10.3	28.8	816	6, 22, 23, 24, 25
<i>Aythya ferina</i>	2	61	1.60				40.1	1,280	19, 22
<i>Aythya fuligula</i>	2	61	1.48				34.1	1,088	22, 23, 26
<i>Branta leucopsis</i>	2	80	3.20				80	3,360	19, 27
<i>Bucephala clangula</i>	2	61	1.08				32.4	1,229	19, 22
<i>Clangula hyemalis</i>	2	80	1.15				30	1,512	19, 27
<i>Melanitta fusca</i>	2	61	1.95				54.7	1,746	19, 22
<i>Mergus merganser</i>	2	61	1.49				46.2	1,375	19, 22
<i>Mergus serrator</i>	2	61	1.38				44.2	1,305	19, 22
<i>Somateria mollissima</i>	2	61	2.27	0.036	2,050		61.4	1,842	6, 19, 22
<i>Somateria mollissima</i>	2	80	2.27	0.036	2,050		65	2,699	6, 19, 27
Order Galliformes									
<i>Alectura lathamii</i>	1	36	2.34			35.3	114.5	2,748	28, 29
<i>Coturnix coturnix</i>	3		0.41	0.069	120	1.565	6.9	228	6, 25, 30, 31
<i>Excalfactoria chinensis</i>	3						3.2	85	31, 32
<i>Gallus domesticus</i> Broiler	3			0.024	3,050		42.8	1,150	6, 33
<i>Gallus domesticus</i> Leghorn	3			0.024	3,050		39.7	1,153	6, 33
<i>Lagopus lagopus</i>	3		0.80	0.065	650		17.5	706	6, 19, 34

TABLE 1. Continued.

Species	HT	L	K _e	K _G	A	M _{10d}	M	RMR _h	Authors
<i>Leipoa ocellata</i>	1	34	1.84			31.4	114	2,216	28, 35
<i>Lophortyx californica</i>	3			0.039	170		7.0	161	6, 36
<i>Phasianus colchinus</i>	3		0.71	0.032	900	3.65	17	367	6, 23, 24, 36
<i>Tetrao urogallus</i>	3		1.28				31.9	1,520	19, 37
Order Charadriiformes, family Charadiidae and Scolopacidae									
<i>Galinago media</i>	3	62	0.65				15	648	19, 38
<i>Haematopus ostralegus</i>	3	54	1.19	0.081	466	3.70	30.93	1,392	39
<i>Limosa limosa</i>	3	53	1.21	0.085	273		27.8	873	40
<i>Numenius arquata</i>	3	53	1.97	0.051	990		55.2	1,603	40
<i>Philomachus pugnax</i>	3	53	0.58	0.092	125		13.4	480	6, 40
<i>Tringa totanus</i>	3	53	0.62	0.070	137		14.2	441	40
<i>Vanellus vanellus</i>	3	53	0.61	0.054	236		17.1	449	40
Order Charadriiformes, family Laridae									
<i>Larus argentatus</i>	5	54	2.13	0.083	1,150		57.4	1,901	41, 42
<i>Larus atricilla</i>	5	29	1.23	0.088	350	5.149	28.4	1,356	25, 30, 43, 44
<i>Larus delawarensis</i>	5	45		0.099	403		34.6	1,345	45, 46
<i>Larus glaucescens</i>	5	49		0.094	927		60.3	1,766	41, 47
<i>Larus occidentalis livens</i>	5	29		0.080	900		65.4	2,119	6, 48
<i>Larus occidentalis wymani</i>	5	33	2.15				58.0	2,060	30, 49
<i>Larus ridibundus</i>	5	61	1.12	0.115	281		26.8	1,460	19, 46, 50
<i>Rissa tridactyla</i>	5	79	1.23	0.097	449		33.1	1,123	51, 52, 53
<i>Anous minutus</i>	5	23	0.48	0.152	117	3.82	16.8	524	7, 54, 55
<i>Anous stolidus</i>	5	23	0.81	0.103	190	5.58	28.52	690	6, 7, 54
<i>Gygis alba</i>	5	28	0.42	0.064	115	3.60	16.1	470	7, 56, 57
<i>Sterna fuscata</i>	5	25	0.55	0.073	205		21.0	529	6, 58
<i>Sterna hirundo</i>	5	54	0.65	0.204	130		14.9	537	6, 23, 58, 59
<i>Sterna paradisaea</i>	5	79	0.55	0.230	105		12.0	547	6, 60
<i>Sterna paradisaea</i>	5	54	0.59	0.196	110		13.03	457	6, 59
<i>Sterna sandvicensis</i>	5	54	1.05	0.175	180		25.25	763	6, 59
Order Charadriiformes, family Alcidae									
<i>Alle alle</i>	5	79	0.77	0.187	125		22.4	1,258	19, 61
<i>Cephus columba</i>	5	49		0.112	425		37.5	1,332	62
<i>Fratercula arctica</i>	5	65	1.07	0.101	390		41.9	1,317	6, 19, 63
<i>Synthliboramphus hypoleucus</i>	5	34					24.8	1,071	64
<i>Uria lomvia</i>	5	79	2.21				74.1	2,240	19, 63
Order Columbiformes									
<i>Columba livia</i>	8		0.88			1.634	15.0	384	30, 65, 66
Order Psittaciformes									
<i>Agapornis personata</i>	8		0.11	0.24	48	2.51	77	67	
<i>Agapornis roseicollis</i>	8		0.12	0.23	52	0.359	2.76	77	30, 67
<i>Aratinga solstitialis</i>	8		0.22				6.02	130	26, 67
<i>Bolborhynchus lineola</i>	8		0.11	0.22	63		2.32	70	67
<i>Enicognathus ferruginous</i>	8		0.24	0.18	187		6.57	190	67
<i>Melopsittacus undulatus</i>	8		0.09				1.67	65	67
Order Passeriformes									
<i>Agelaius phoeniceus</i>	8	35	0.32				3.50	103	68
<i>Carduelis tristis</i>	8	40					1.51	72	69
<i>Passerculus sandwichensis</i>	8	30					2.05	158	70

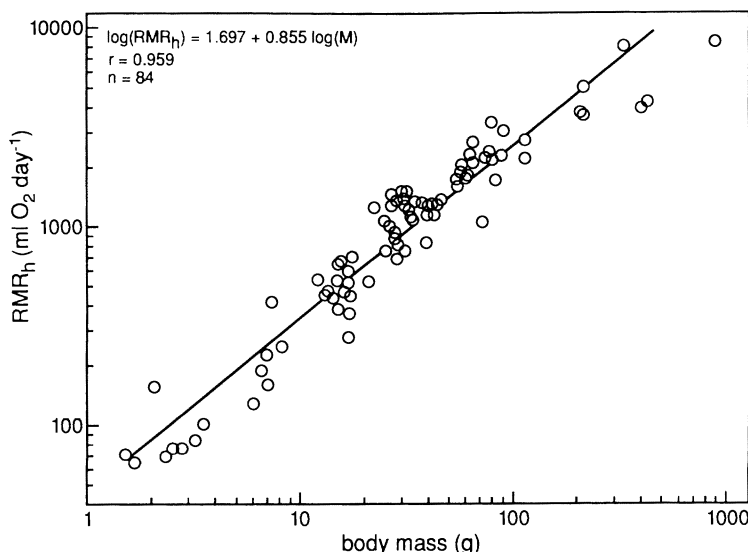


FIGURE 1. Regression of hatchling resting metabolism plotted against fresh body mass of the hatchling. Data from Table 1. Line calculated using least square statistics on the logarithmically transformed variables (Eq. 1).

Hatchling resting metabolism is related to yolk-free dry mass (Fig. 2) as follows:

$$\log(\text{RMR}_h) = 2.317 + 0.766 \log(M_{\text{yfd}}) \quad (2)$$

($r = 0.938$, $P < 0.001$, $n = 18$).

Some variance in mass-independent hatchling resting metabolism (when calculated on the basis of fresh body mass, not taking phylogeny into account) is statistically related to hatchling type (ANOVA, $F = 3.363$, $P = 0.008$, $n = 84$). However, there exists no simple linear relationship between mass-independent hatchling resting metabolism and the level of altriciality when using either fresh body mass ($r = -0.124$, $P = 0.263$, $n = 84$; Fig. 3A), or yolk-free dry mass ($r = 0.141$, $P = 0.931$, $n = 18$; Fig. 3B). When mass-independent metabolism is calculated on the basis of the phylogenetic group-specific allometric equations from Table 2, hatchling type contributes nothing to the explanation of the variance left

(ANOVA, $F = 0.401$, $P = 0.807$, $n = 67$), mainly because each phylogenetic group is made up of largely similar hatchling types.

Equations relating embryonic growth rate with hatchling fresh body mass (Table 3) and equations relating postnatal growth rate with asymptotic body mass (Table 4) are presented for all species and for each phylogenetic group also represented in Table 2. However, in Table 4 the Anseriformes and the Psittaciformes are omitted as too few data were available for analysis (3 and 4, respectively). The relation for the Galliformes was not significant ($r = -0.782$, $P = 0.066$, $n = 6$) and is likewise not included in Table 4. For postnatal growth, allometric equations based on extensive data are available for Laridae (Drent and Klaassen 1989) and Charadriidae and Scolopacidae (Beintema and Visser 1989). For these phylogenetic groups, we present the published equations in Table 4.

1, Bucher et al. (1986); 2, Bucher et al. (in press); 3, Taylor (1985); 4, Vleck (1978); 5, Brown and Adams (1988); 6, Ricklefs (1973); 7, Pettit et al. (1984b); 8, Pettit et al. (1982a); 9, Vleck and Kenagy (1980); 10, Rahn et al. (1984); 11, Ricklefs et al. (1980); 12, Ricklefs (1989); 13, Ricklefs and Roby (1983); 14, Pettit et al. (1982b); 15, Pettit et al. (1984a); 16, Ackerman et al. (1980); 17, Bech et al. (1982); 18, Bech et al. (1988); 19, Cramp (1983); 20, Bartholomew and Goldstein (1984); 21, Bartholomew and Goldstein (in Vleck and Vleck 1987); 22, Koskimies and Lahti (1964); 23, Hoyt and Rahn (1980); 24, Romanoff (1967); 25, Ricklefs (1977); 26, Bucher and Bartholomew (1984); 27, Steen and Gabrielsen (1986); 28, Vleck et al. (1984); 29, Booth (1985); 30, Vleck and Vleck (1987); 31, Matthew (1982); 32, Bernstein (1973); 33, Kuenzel and Kuenzel (1977); 34, Aulie (1976); 35, Booth (1984); 36, Koskimies (1962); 37, Hissa et al. (1983); 38, Steen et al. (in prep.); 39, Klaassen (in prep.); 40, Visser (in prep.); 41, Drent (1970); 42, Spaans (1971); 43, Dawson et al. (1972); 44, Schreiber and Schreiber (1980); 45, Dawson et al. (1976); 46, Glutz and Bauer (1982); 47, J. Ward (unpubl.); 48, Dawson and Bennett (1980); 49, Dawson and Bennett (1981); 50, Palokangas and Hissa (1971); 51, Bech et al. (1984); 52, Klaassen et al. (1987); 53, Gabrielsen et al. (in prep.); 54, Pettit and Whitow (1983); 55, Langham (1983); 56, Pettit et al. (1981); 57, Dorward (1963); 58, Ricklefs and White (1981); 59, Klaassen and Zwaan (in Drent and Klaassen 1989); 60, Klaassen et al. (1989c); 61, Konarzewski et al. (in prep.); 62, Drent (1965); 63, Bech et al. (1987); 64, Eppley (1984); 65, Vleck et al. (1979); 66, Ar et al. (1987); 67, Bucher (1983); 68, Carey et al. (1982); 69, Mayer et al. (1982); 70, Williams and Prints (1986).

TABLE 2. Equations relating hatchling resting metabolism (RMR_h , ml O_2 day $^{-1}$) with fresh body mass (M , g; $\log(RMR_h) = a + b \log(M)$) for 6 phylogenetic groups containing at least 6 data points.

Phylogenetic group	a	b	n	r*
Order Procellariiformes	1.838	0.785	16	0.965
Order Anseriformes	1.054	1.289	13	0.919
Order Galliformes	1.506	0.958	10	0.972
Order Charadriiformes				
Family Laridae	1.601	0.955	16	0.927
Family Charadriidae and Scolopacidae	1.596	0.951	7	0.928
Order Psittaciformes	1.599	0.737	6	0.958

* In all cases $P < 0.005$.

Regressing mass-independent hatchling metabolism on mass-independent embryonic growth rate (Fig. 4) results in a positive correlation ($r = 0.284$, $P = 0.028$, $n = 60$) if only those species are used for which phylogenetic group-specific allometric equations are available. For the six phylogenetic groups treated here, a clear correlation between embryonic growth rate and hatchling metabolism is apparent within the phylogenetic group only in the case of the Laridae ($r = 0.686$, $P = 0.010$, $n = 13$). The same analysis for mass-independent postnatal growth rate with hatchling metabolism (Fig. 5) revealed an increase in metabolism with growth rate ($r = 0.465$, $P = 0.011$, $n = 29$) if only those species are used for which phylogenetic group-specific equations are available.

Mass-independent hatchling metabolism is positively correlated with latitude both when Eq. 1 is used on all species for the calculation of mass-independent hatchling resting metabolism ($r = 0.558$, $P < 0.001$, $n = 56$) and when the phylogenetic group-specific allometric equations (Table 2) are used ($r = 0.407$, $P = 0.003$, $n = 50$; Fig. 6). Within the order Procellariiformes this correlation also is apparent ($r = 0.552$, $P = 0.033$, $n = 15$). Within the family Laridae, the only other phylogenetic group with enough data points and variation in latitude to allow the analysis, the relation is not significant ($r = 0.442$, $P = 0.131$, $n = 13$), although for the subfamily Stercorariinae it is ($r = 0.899$, $P = 0.002$, $n = 8$).

DISCUSSION

BODY SIZE

The exponent of the allometric equation relating hatchling resting metabolism with fresh body mass (0.855, Eq. 1) is well above the range of values so far found in adult birds (0.67–0.75).

The allometric equations within the phylogenetic groups (Table 2) show exponents in the range 0.7–1.3 and slightly higher than the exponents found in phylogenetic analyses of adult birds (Bennett and Harvey 1987). However, any attempt to explain the value of the exponent in the allometric relations of resting metabolism by a general principle is likely to fail (Calder 1987, Heusner 1987). One should, therefore, take Medawar's (1950) advice, and ask whether the relationships found are expedient and useful.

Because the relation between resting metabolism and body mass of hatchlings (Eq. 1) is so different from that in adult birds, one should be careful to use the appropriate equation before attempting to generalize metabolic processes on a mass-specific basis. Heusner (1983, 1985) proposed dividing adult resting metabolic rate by body mass to the power 0.67 to allow direct comparison between species. Applying this procedure for hatchling resting metabolic rate without adjusting the exponent from 0.67 to 0.86 (as empirically found here) would overestimate mass-independent hatchling resting metabolic rate values.

PHYLOGENETIC CATEGORY

Discrimination for phylogenetic groups in adult birds results in different allometric relations for resting metabolism (e.g., Bennett and Harvey 1987). As shown by analysis of covariance (see results and Table 2), this also holds for hatchlings. In addition to differences in embryonic and postnatal growth rate (Tables 3, 4), each phylogenetic group has its specific habitat, mode of prey capture, daily rhythm, etc. Indeed, in adult birds it has been shown that confounding associations exist between resting metabolic rate among families and these behavioral and eco-

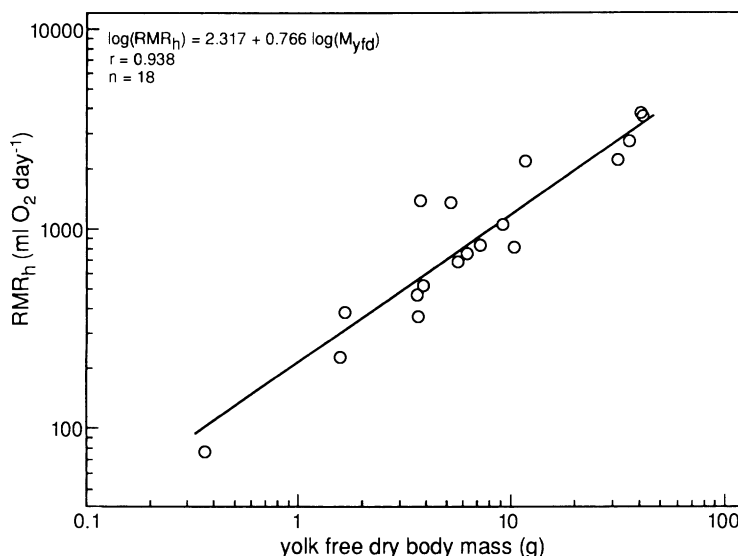


FIGURE 2. Hatchling resting metabolism plotted against hatchling yolk-free dry body mass. Data from Table 1. The least square regression line on the logarithmically transformed variables is indicated (Eq. 2).

logical variables. Probing analyses such as Bennett and Harvey (1987) conducted on the resting metabolism of adult birds are not yet possible for hatchlings as too few data are available. Thus, the metabolic implications of phylogeny related characteristics are not further examined here. By using the phylogenetic group-specific allometric equations from Tables 2, 3 and 4, variations in hatchling resting metabolic rate and embryonic and postnatal growth rate due to accidents of phylogeny are largely corrected for in our analyses.

HATCHLING MATURITY AND BODY COMPOSITION

In an analysis of hatchling mass-independent resting metabolism, Bucher (1987) concluded that the level of metabolism at hatching varied as much between as within Nice's categories. This agrees with Rahn and Whittow's (1984) conclusion based on more limited data. Although no correlation exists, analysis of variance reveals a significant effect of hatchling type on hatchling resting metabolism, when phylogeny is not taken into account. When this is incorporated, no unambiguous effect of ontogenetic type on hatchling resting metabolism is apparent in our analysis. This would suggest that ontogenetic novelties, as far as they are metabolically expressed, arise in phylogenetic steps and not within phylogenetic lines.

Hatchlings of altricial species differ dramatically from precocial species in their yolk and water content (Romanoff 1944; Nice 1962; Ricklefs 1974, 1977; Blem 1976; Ar and Yom-Tov 1978; Ricklefs et al. 1978; Ar and Rahn 1980; Carey et al. 1980; Carey 1983; Pettit et al. 1984b; Rahn et al. 1984; Sotherland and Rahn 1987). Water is metabolically inactive, and yolk has not been shown to exhibit any oxidative capacity (Steen and Gabrielsen 1986). Therefore, it has been practice to use yolk-free dry mass in metabolic studies on hatchlings (Bucher 1986, 1987; Vleck and Vleck 1987) and embryos (Hoyt 1987). However, yolk reserves in hatchlings do increase metabolic rates (Klaassen et al. 1987), although the relationship between the absolute amount of yolk reserve and its metabolic effect remains unanalyzed. Water per se may be metabolically inactive, but this does not imply that the metabolic function of tissue is independent of water content. For example, growth rates of chicks have been found to be closely related with water content (Ricklefs 1967b, O'Connor 1977, Ricklefs and Webb 1985) and water content might therefore be closely linked to metabolic performance. This is relevant to the concept of describing water content as an index of maturity (see Ricklefs 1979, Ricklefs and Webb 1985). Finally, in reptilian embryos the hydric conditions of the egg affect growth and metabolism (Vleck and Hoyt, in press). In any case, analysis of hatchling metab-

olism with regard to ontogenetic type on the basis of yolk-free dry mass likewise failed to reveal any relationship. Thus, we abstain from correction for differences in composition between altricial and precocial hatchlings by subtracting yolk and water mass from the live mass.

EMBRYONIC AND POSTNATAL GROWTH RATE

A correlation between hatchling resting metabolism and postnatal growth rate was earlier shown by Drent and Klaassen (1989). Additional support comes from the comparison of avian and reptilian embryos, where both rate of growth and metabolism are much lower in the latter (Vleck and Hoyt, in press). Why resting metabolism is coupled to growth rate can be understood when we assume that a change in growth rate necessitates a rescaling of the metabolic machinery of an animal. Kirkwood and Prescott (1984) showed, in an interspecific comparison of mammals and birds, that a positive relation exists between growth rate and gut size. The studies of Daan et al. (1989, 1990) on the relation between animal composition and resting metabolism in adult birds and of Koong et al. (1982) on mammals, support the idea that these changes in the metabolic machinery (including organ size) change the resting metabolic rate.

As an alternative to the functional explanation of the relation between resting metabolism in hatchlings and growth rate given above, it could be argued that the relative size of the yolk sac, which is also used for catabolic purposes after hatch, is related to embryonic and postnatal growth rate and thus has a direct effect on metabolism. However, the metabolic effect of the yolk reserves in Black-legged Kittiwake (*Rissa tridactyla*) was estimated at only 6% of the hatchling resting metabolic rate which was 113% of the expected value (Klaassen et al. 1987). As deviations from expected hatchling resting metabolic rate exist of -35-72% (Figs. 4, 5), it is very unlikely that variations in the state of the yolk reserve are the sole source for the existing differences in mass-independent hatchling metabolism. Furthermore, no correlation exists between hatchling type and mass-independent hatchling metabolism, although post-hatch yolk reserves increase with increasing precociality.

Satisfying models have been generated which describe the energy expenditure of embryos during embryonic development, on the basis of both

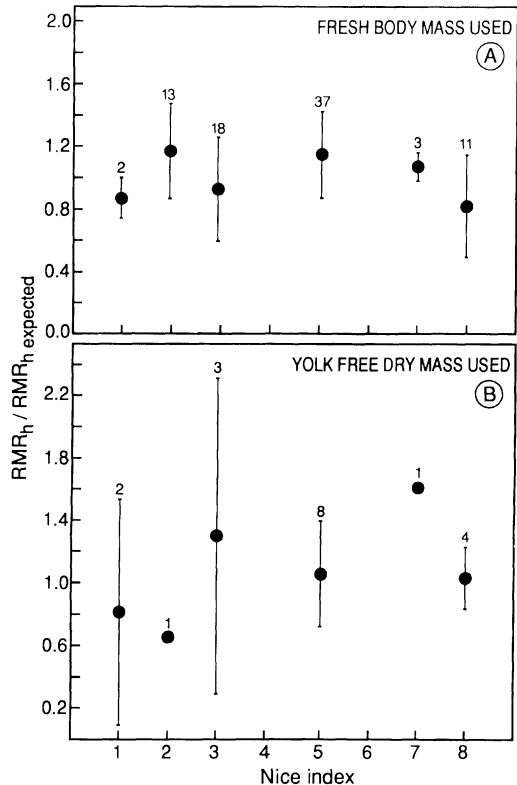


FIGURE 3. Hatchling mass-independent metabolism calculated using hatchling fresh body mass (A) and hatchling yolk-free dry body mass (B) as function of hatchling type, which is the altriciality gradient according to the classification of Nice (1962; for coding see text). Standard deviations and sample sizes are indicated.

embryo mass and growth rate (Vleck et al. 1980, Hoyt 1987). Although supporting the finding that hatchling resting metabolism shows a positive relation with growth rate, costs of growth as estimated in these models are low. However, this may be due to the statistical impossibility of reliably separating the costs of maintenance and growth in these simple models (see also Hoyt 1987, for a discussion on the sources of error).

The next important step in furthering our knowledge of growth-related changes in resting metabolism is to study variation in resting metabolism after hatching. This is of compelling interest because the resting metabolic rate constitutes approximately half of the total energy requirements of the growing chick (Drent and Klaassen 1989). An implication of the fact that

TABLE 3. Equations relating embryonic growth rate (K_e , g day⁻¹) with fresh body mass (M , g; $\log(K_e) = a + b \log(M)$) for all species and the 6 phylogenetic groups in Table 2.

Phylogenetic group	a	b	n	r*
All species	-1.201	0.803	70	0.959
Order Procellariiformes	-1.453	0.847	15	0.992
Order Anseriformes	-1.268	0.902	13	0.967
Order Galliformes	-0.838	0.572	6	0.982
Order Charadriiformes				
Family Laridae	-1.408	0.978	13	0.922
Family Charadriidae and Scolopacidae	-1.250	0.893	7	0.987
Order Psittaciformes	-1.221	0.722	6	0.995

* In all cases $P < 0.001$.

resting metabolic rate is positively correlated with growth rate is that growth costs are not solely the summation of the costs of synthesis and deposition of tissue. The growth-rate associated change in resting metabolism also has to be accounted for. It was Ricklefs' (1983) belief that the costs of postnatal growth are not a substantial contribution to the daily energy needs of chicks. Based on work on the Sooty Tern (*Sterna fuscata*), Ricklefs and White (1981) modeled the consequences of a doubling of the growth rate. They concluded that, near the inflection point (20 days), this would entail a daily energy increment of 42 kJ, an increase of only one-third compared to the level normal at that age. However, assuming that the inter-species relationship between growth rate and resting metabolic rate also applies to intraspecific variation, Drent and Klaassen (1989) recalculated the increment in energy needs for the Sooty Tern to 76 kJ/day, about twice the level calculated by Ricklefs and White (1981; Fig. 7).

The energetic consequences of alterations in growth rate have here been discerned at the inter-

specific level. Our provisional working hypothesis is that this coupling is achieved in the course of evolution, whereby the resting metabolism is tuned to growth rate (and possibly other physical and environmental circumstances). Extrapolation to the intra-specific level is thus not yet permissible.

LATITUDE

Increases in embryonic growth rate and postnatal growth rate appear to go hand in hand with increased latitude of hatching ($r = 0.319$, $P = 0.024$, $n = 50$ and $r = 0.636$, $P < 0.001$, $n = 29$ respectively, for the species within the phylogenetic groups in Tables 3 and 4). That chicks of temperate and arctic bird species tend to have higher growth rates than their tropical relatives was shown by Ricklefs (1968, 1976), Björnhag (1979) and Langham (1983). These variations in growth rates have been related to such factors as mortality rate (high in tropics), food availability (high in the Arctic; Lack 1968) and length of breeding season (long in tropics; Ricklefs 1984),

TABLE 4. Equations relating postnatal growth rate (K_G) with asymptotic body mass (A , g; $\log(K_G) = a + b \log(A)$) for all species and the 6 phylogenetic groups in Table 2 and 3, with the exception of the Anseriformes and Psittaciformes for which too few data points were available and the Galliformes for which the relationship was not significant. For the Laridae, Charadriidae and Scolopacidae equations available from studies on more extensive data sources were used.

Phylogenetic group	a	b	n	r*
All species	-0.192	-0.348	49	-0.714
Order Procellariiformes	-0.415	-0.337	8	-0.848
Order Charadriiformes				
Family Laridae	-0.024	-0.345	26	-0.870 ¹
Family Charadriidae and Scolopacidae	-0.390	-0.312	19	-0.866 ²

* In all cases $P < 0.05$.

¹ From Drent and Klaassen 1989.

² From Beintema and Visser 1989.

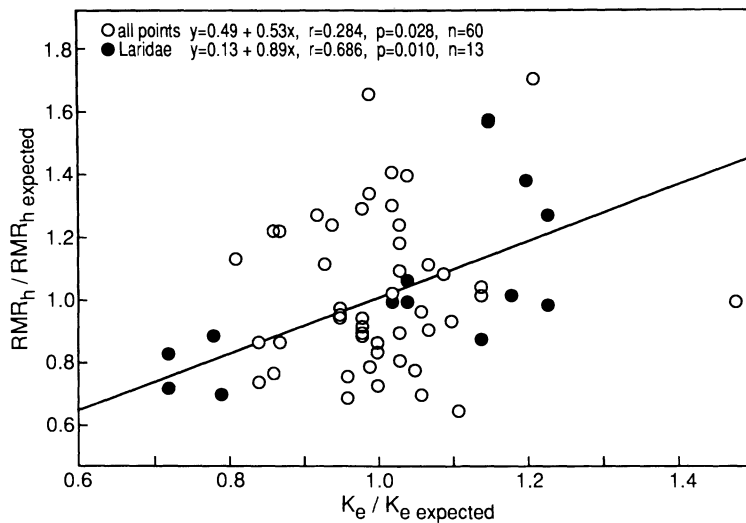


FIGURE 4. Relationship between mass-independent hatchling metabolism and mass-independent embryonic growth rate. Closed symbols: Laridae; open symbols: all other species for the phylogenetic groups in Table 3. Indicated is the calculated least square regression line.

which all favor increasing growth rates with latitude.

In addition, hatchling metabolism likewise increases as place of birth approaches the poles (Fig. 6). Post-hatch growth rate also is higher when embryonic growth rate is high. This relationship is significant for the species within the

phylogenetic groups in Tables 3 and 4 ($r = 0.474$, $P = 0.017$, $n = 25$). The relation is significant within a phylogenetic group only for the Laridae ($r = 0.792$, $P = 0.002$, $n = 12$). Other studies supporting a close link between embryonic and postnatal growth include Lack (1968), Drent (1975) and Drent and Klaassen (1989). Thus,

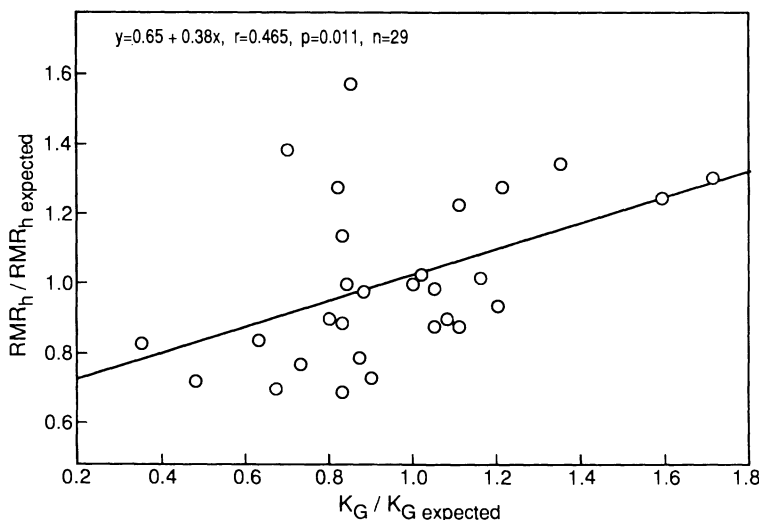


FIGURE 5. Relationship between mass-independent hatchling metabolism and mass-independent postnatal growth rate for all species of the phylogenetic groups in Table 4. The calculated least square regression line is indicated.

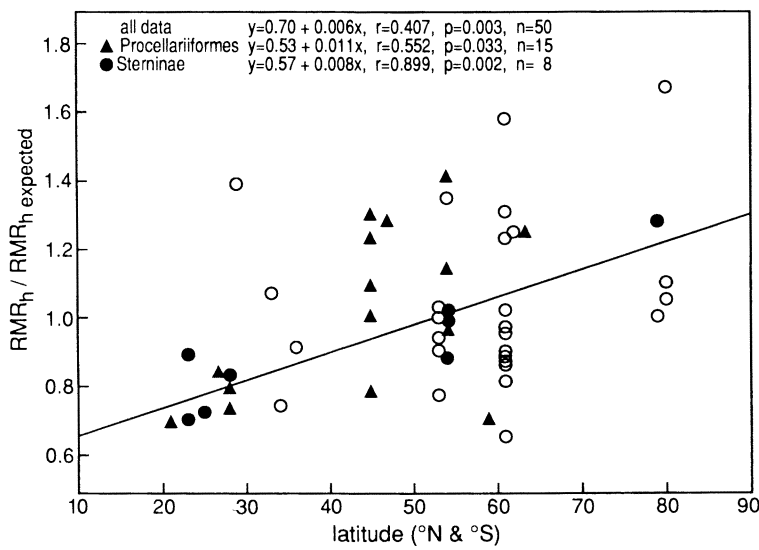


FIGURE 6. Mass-independent hatchling metabolism plotted as a function of latitude for all species of the phylogenetic groups in Table 2 (closed dots: Sterninae; closed triangles: Procellariiformes; open dots: all other species). The least square regression line is drawn over all data points.

hatchling resting metabolism, embryonic growth rate, postnatal growth rate and latitude all appear interrelated.

Several studies have established a relation between hatchling metabolism and latitude (Ricklefs 1976; Bryant and Hails 1983; Rahn and Whittow 1984; Taylor 1985; Brown and Adams 1988; Klaassen et al. 1989a, 1989c). Also, in adult birds a positive correlation exists between latitude and resting metabolism (Weathers 1979, Hails 1983, Ellis 1984). Clearly, latitude in itself is not important to the bird, but is here used to subsume important environmental information. Environmental conditions for three species of terns at three different latitudes are illustrated in Figure 8. Ambient temperature decreases towards the pole while the yearly fluctuation in ambient temperature increases. These two latitude-coupled meteorological phenomena together with the change in day length contribute to the shortening of the breeding season at high latitudes.

The adaptive advantage of the latitudinal difference in resting metabolism for adults has been interpreted as a mechanism of avoiding heat stress by reducing endogenous heat production (Weathers 1979, Ellis 1984). Evaporative heat loss is a major pathway in dissipating heat but operates at the expense of water. An increase of evaporative heat loss of a chick can thus entail

a disruption in water economy necessitating adjustments of parental behavior (some species deliver water directly; others provide water only in the form of food items). Low-latitude hatchlings

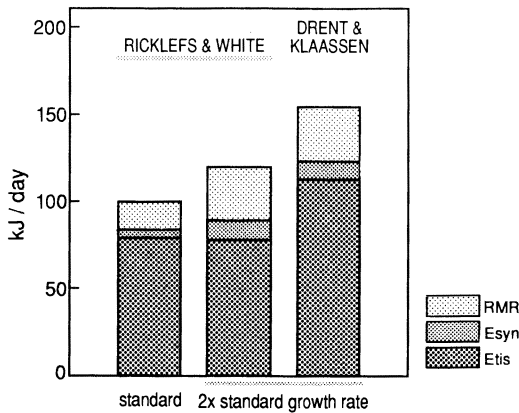


FIGURE 7. Comparison of daily net energy requirement (exclusive of activity) for growth in the Sooty Tern (*Sterna fuscata*) at 20 days of age estimated for normal field conditions (standard; Ricklefs and White 1981) and as predicted for a doubling of growth rate by the model of Ricklefs and White (1981) or alternatively according to Drent and Klaassen (1989; calling for the adjustment of RMR). Net energy requirement is partitioned into resting metabolic rate (RMR), energy deposited in body tissue (E_{syn}) and energy required for synthesis (E_{tis}).

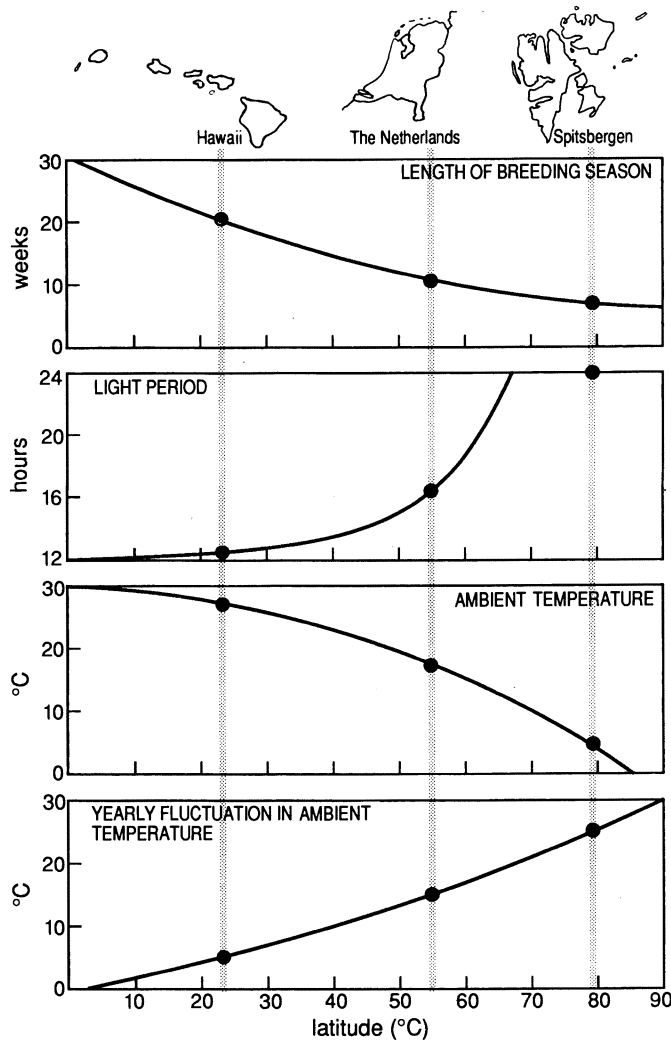


FIGURE 8. Schematic overview of implications of latitude for breeding birds: from equator to pole length of breeding season, daylight period, ambient temperature and its yearly fluctuation are shown. The trend lines are interrupted at 26°N (Hawaii), 54°N (Netherlands) and 79°N (Spitsbergen) as depicted in the insets. These exemplify sites where terns representative for the geographical region breed (*Sterna fuscata*, *S. hirundo* and *S. paradisaea*, respectively).

seem to have metabolic rates that are 30% below normal for their mass (Fig. 6). This would yield a 30% reduction in evaporation water loss if ambient temperature approaches body temperature (Fig. 9), which may occur at low latitudes.

An environmental factor closely linked with latitude is air temperature. Ellis (1984) and Kersten and Piersma (1987) argued that relatively high resting metabolism is associated with high working capacity, which might be advantageous in the arctic, where seasons are short and harsh

weather prevails. Relevant to the hatchling is the thermogenic potential, i.e., the metabolic scope that can be deployed in producing heat to maintain body temperature. Assuming that for hatchlings a sustained level of two times RMR_b is a realistic estimate of this potential (Ricklefs 1989), we calculated the impact that the adjustment of RMR_b exerts on the lower temperature threshold of the domain of thermoregulation. The lower limit at which the hatchling can maintain body temperature when exposed to the environment

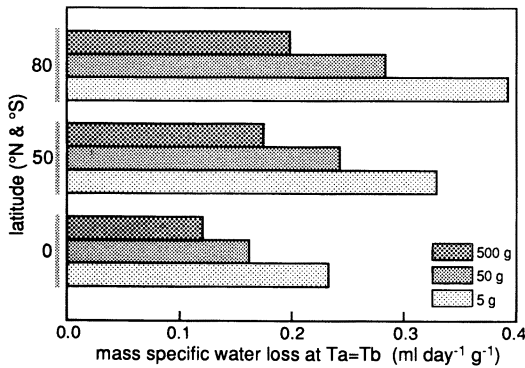


FIGURE 9. Comparison of rate of evaporation (given as $\text{ml day}^{-1} \text{g}^{-1}$ body mass) required to dissipate resting metabolic heat production when ambient temperature (T_a) equals body temperature (T_b) assuming all heat is lost by evaporation. This is calculated for 3 categories of hatchling body mass (5, 50 and 500 g) typical for polar (80°), mid-latitude (50°), where RMR_h matches expectations according to the all data Eq. in Fig. 6) and equatorial (0°) localities (see text).

for any length of time is expanded by 4, 8 and 18°C for typical polar hatchlings compared with equatorial birds of the same body mass (5, 50 and 500 g, respectively) (Fig. 10). It could be argued that most neonates will be brooded by the parent during extreme conditions, but exposure to the elements is a daily occurrence and we presume that under polar conditions the hatchlings do not have the option of allowing body temperature to fall to ambient levels. Still, the lower environmental temperature limit for maintaining body temperature for hatchlings with body masses most common in polar environments (about 50 g) is well above prevailing ambient temperatures at those latitudes (Fig. 8). However, solar radiation regularly elevates operative temperatures over air temperatures by more than 20°C in the arctic (Klaassen et al. 1989b).

In addition to adjustment of resting metabolic

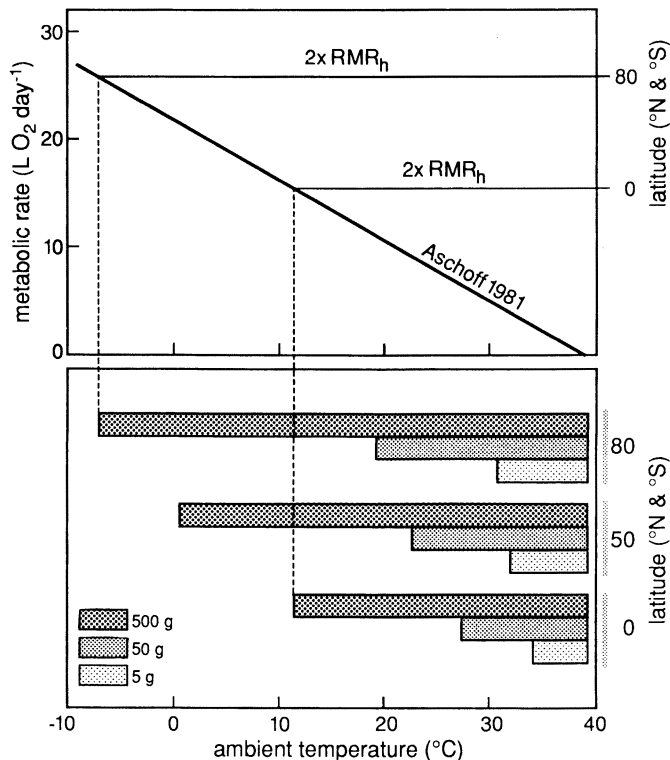


FIGURE 10. Implications of latitude for hatchling thermoregulation. Upper panel shows derivation of lower limit of the domain of thermoregulation, defined as the range of ambient temperature where the hatchling can maintain stable body temperature with a modest thermogenic output equivalent to $2 \times \text{RMR}_h$ (Ricklefs 1989), presented for hatchlings of 500 g body mass from equatorial (0°) and polar (80°) localities. The metabolic levels concerned have been entered according to Eq. 1 adjusted for the latitudinal effect (see Fig. 6). Threshold temperatures are found graphically by finding the point where the metabolic level intercepts the expected heat

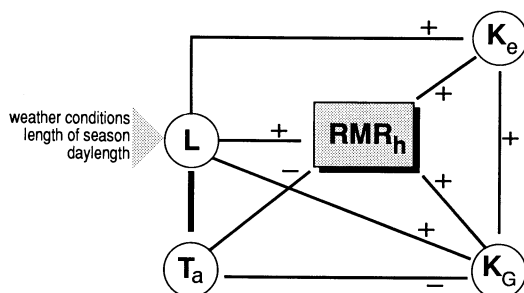


FIGURE 11. Schematic overview of interrelations between variables impinging on hatchling resting metabolic rate (RMR_h): ambient temperature (T_a), latitude (L) with associated phenomena, embryonic growth rate (K_e), and postnatal growth rate (K_G). Arrows indicate the probable direction of dependence. Adjustments of the variables K_e , K_G , and RMR_h are viewed as direct or indirect adaptive responses to environmental pressures.

rate as an evolutionary adaptation, it is conceivable that a direct effect of cold on the developing embryo can influence metabolic rate. Dawson (1984) noted that incubation temperatures may be periodically influenced by ambient temperatures. Geers et al. (1983) found increased metabolic rates in hatchlings of the domestic fowl, which were subjected to cold shocks during the last week of incubation. Although effects of cooling and heating of avian embryos are complex and depend on the intensity, duration and timing of exposure (Drent 1973, Dawson 1984), the data of Geers et al. (1983) fit the general trend of increasing hatchling resting metabolic rate with latitude. Postnatal growth rate as well is inversely related to ambient temperature during incubation (Geers et al. 1983) and the post-hatch period (Kleiber and Dougherty 1934, Osbaldiston 1966, Murphy 1985, Aulie 1977, Barré et al. 1985). It therefore is impossible to distinguish whether hatchling resting metabolism is affected directly by temperature or whether it changes as a result of a shift in growth rate itself triggered by temperature.

CONCLUSION

In this review we have developed a functional explanation for the link between latitude and em-

bryonic and postnatal growth rate in the context of hatchling resting metabolism (summarized in Fig. 11). Characterizing the microclimatic conditions actually experienced by the hatchlings, rather than simply latitude, is needed to broaden our understanding. Other variables deserve further study. There is a hint, for example, that type of food brought to the chick might necessitate adaptations in the level of resting metabolism (Bennett and Harvey 1987). Although there seem to be no criteria to ascertain the causal links in a rigorous fashion, we argue that adjustment of resting metabolic rate is at the core of the adaptation of the organism to its environment.

ACKNOWLEDGMENTS

It is a pleasure to look back at the period spent by one of us (M.K.) in the stimulating environment of the avian physiology group at the University of Trondheim, Norway, where in discussions with Claus Bech many of the ideas presented here may be said to have reached the pipping stage. That this review has achieved hatching is due in no small measure to the friendly atmosphere generated during the "Physiology of Cold Adaptation in Birds" conference organized by Claus Bech and Randi Reinertsen, where we were brought into contact with Theresa Bucher. Subsequently, we benefitted from the generous response and the help of many investigators who placed their unpublished data at our disposal (Bill Buttemer in addition to those listed in Table 1). We also thank Carol Vleck who, in addition to Claus Bech and Theresa Bucher, made many valuable suggestions during writing of the manuscript, and Dick Visser for drawing the figures. Two anonymous reviewers made valuable comments on our manuscript.

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loss for birds of this size calculated according to Aschoff's (1981) equation for adult non-passerines (assuming body temperature equals 39°C). The values found for the 500 g hatchlings are depicted in the bar graph below and show that for the polar representative the metabolic adjustment extends the zone of ambient temperature tolerated by 18°C compared to the equatorial bird. Values similarly derived for a mid-latitude station (50°, where RMR_h matches expectation according to Eq. 1) and including hatchlings of 50 g and 5 g are also shown.

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